Analysis of morphology to determine primary sister-taxon relationships within coleoid cephalopods

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Abstract: Although most families of living coleoid cephalopods are well defined, phylogenetic relationships among them are controversial. A necessary first step toward analyzing the phylogeny of decapod families is the determination of proper outgroups to polarize characters. The cladistic position of the Vampyromorpha is of particular interest. Toward this goal, we have examined 50 morphological characters in 24 species from 17 families. The material examined included representatives from the oegopsids, myopsids, sepioids and sepiolids, cirrate and incirrate octopods, and *Vampyroteuthis*. At this level, the characters were polarized either by comparison with *Nautilus*, or, for a few, by ontogenetic sequence or the fossil record. We found that of these 50 characters, 25 could not be used with confidence because of problems primarily involving character independence, apomorphic "loss," or assessment of homology/homoplasy. The states of three characters could be assumed to be ordered. Only ten characters were unambiguously informative as defining synapomorphies at the ordinal level. The resulting consensus of most-parsimonious trees is: (((oegopsid + myopsid + sepioid + sepiolid)(((cirrate)(incirrate)) vampire))(nautilus)).

Although most families of living coleoid cephalopods are well defined, phylogenetic relationships among them are controversial. Our understanding of cephalopod phylogeny is based mostly on the work of Naef (1921-1923; 1928). Advances in cephalopod systematics since the 1920s have mainly described new orders, families, genera, and species. The unraveling of the evolutionary pathways of this group has remained nearly stagnant. The phylogenetic classification presented by Voss (1977), summarized from much earlier authors, has been widely followed by most workers studying extant cephalopods (*e. g.* Roper *et al.*, 1984; Nesis, 1987; Mangold and Portmann, 1989; and the many researchers who have used their works). Many paleontologists, however, have not been comfortable with this classification. Relationships among the decapods have also been questioned (*e. g.* J. Z. Young, 1977; Fioroni, 1981; Boletzky, 1993a). Recently, Berthold and Engeser (1987) performed a phylogenetic analysis of the coleoid cephalopods and the resulting classification was quite different from that given by Voss. Perhaps the most important difference is that the myopsid squids (Loliginidae and Pickfordiateuthidae) were found to be more closely related to the cuttlefishes than they are to the other squids. Other recent attempts based on limited sets of characters (*e. g.* Clarke and Maddock, 1988; Clarke, 1988; Khromov, 1990) have not produced a credible genealogy of coleoid cephalopods.

The fossil record of coleoid cephalopods is generally meager with the exception of the hard structures of belemnites. Indeed, Donovan (1977: 45) concluded that "The phylogeny of living coleoids has to be compiled from hopelessly inadequate paleontological evidence. It is not surprising that attempts to work it out have been made at long intervals and have been more or less unconvincing." Much undescribed and unexamined fossil "teuthoid" material exists in museums (Donovan, 1977). Perhaps sufficient material exists that a convincing case for relationships could be made if interpreted within the general framework of a genealogy based on the analysis of Recent cephalopods.

Our virtual lack of progress in understanding cephalopod evolution is due to the fact that: (1) no broad-based morphological study has been attempted since Naef's work, although several dissertations on the comparative morphology of particular structures have produced valuable information (*e. g.* Toll, 1982, teuthoid gladius; Brakoniecki, 1986, loliginid hectocotylus; Hess, 1987, spermatophores; S. Candela, University of Miami, in preparation, beaks); (2) only a single molecular study of higher-level systematics has been published (Bonnaud *et al.*, 1994), and its results demonstrated the difficulty in selecting proper genes for analysis; and (3) studies using cladistic techniques have been few and these have dealt with genera within a family (*e. g.* Voss and Voss, 1983) or between just a few families

American Malacological Bulletin, Vol. 12(1/2) (1996):91-112

(R. E. Young and Harman, in press). Cladistic techniques on a broad basis have not been properly used by either neontologists or paleontologists.

As a first-step toward analyzing cephalopod phylogeny we have chosen a top-down approach in order to determine outgroups for polarizing characters at lower phylogenetic levels. Our goals in this paper are: (1) to determine if the major coleoid taxa, Cirrata, Incirrata and Decapoda, are monophyletic (the monophyly of the Vampyromorpha is already established by its monotypy); and (2) to determine the relationships among these four taxa. Achievement of these goals will determine the placement of the Vampyromorpha and whether or not the Octopoda is monophyletic. We have examined 50 morphological characters in 24 species from 17 families to determine these ordinal and subordinal relationships. The material examined included representatives from the oegopsids, myopsids, sepioids and sepiolids, cirrate and incirrate octopods, and *Vampyroteuthis*.

MATERIALS AND METHODS

As terminal taxa for this study, we selected 17 families which we felt were representative of the putative major groups of extant coleoids although we did not include families that have highly derived autapomorphies (*e. g.* the coelomic specializations of cranchiid squids). Most families, other than monotypic families, were represented by two species often in two genera (Table 1). These species were examined for each character from specimens in the USNM collections (National Museum of Natural History, Washington, D. C.). In addition, a large variety of individuals was examined to determine the structure of a character in order to refine the character definition.

We surveyed 50 characters for each of the terminal taxa. The characters and their states are presented below in the Results section. Almost all character states were assessed by direct examination of specimens. In a few cases, such as neuroanatomy of the brain, we accepted reliable observations from the literature. As discussed below, half of the characters were eliminated from final analyses because of questions about independence, problems with assessing homology versus homoplasy, or our inability to define and assess unambiguous character states.

Nautilus is the clear outgroup for the coleoids. However, because *Nautilus* is so far removed from the coleoids morphologically, many of the ingroup characters are not applicable to it. In order to incorporate information from paleontology and ontogeny for polarity determination, we designated the outgroup as *Nautilus*/ancestral-coleoid. Thus, when a character was not applicable to *Nautilus* but could be polarized by fossil or developmental observations,

Table 1. Species examined for all characters. ML = mantle depth.

FAMILY (HIGHER TAXA) Species	USNM Catalog No.	ML	Sex
BATHYTEUTHIDAE (OEGOPSIDA)			
Bathyteuthis abyssicola Hoyle, 1885	885673	63	female
	577804	40	male
	577804	53	female
BOLITAENIDAE (INCIRRATA)			
Japetella diaphana Hoyle, 1885	885674	41	juv.
	575636	80	female
J. heathi (Berry, 1911)	813756	40	juv.
ENOPLOTEUTHIDAE (OEGOPSIDA)			
Abralia trigonura Berry, 1913	730630	41	female
	730630	35	male
Enoploteuthis anapsis Roper, 1964	728753	62	male
	728753	81	male
	728754	72	female
	728754	40	female
GONATIDAE (OEGOPSIDA)			
Gonatus antarcticus Lönnberg, 1898	885675	139	female
LOLIGINIDAE (MYOPSIDA)			
Loligo pealei Lesueur, 1821	814246	160	male
Lolliguncula brevis (Blainville, 1823)	729175	104	female
Sepioteuthis sepioidea (Blainville, 1823)	814383	140	female
NAUTILIDAE (NAUTILOIDEA)			
Nautilus pompilius Linné, 1758	678868	70	female?
OCTOPODIDAE (INCIRRATA)			
Octopus vulgaris Cuvier, 1797	577100	48	female
OCYTHOIDAE (INCIRRATA)			
Ocythoe tuberculata Rafinesque, 1814	727831	62	female
OMMASTREPHIDAE (OEGOPSIDA)			
Illex illecebrosus (Lesueur, 1821)	885676	115	male
	885676	128	juv.
Ommastrephes bartramii (Lesueur, 1821)	814773	109	juv.
	814773	113	---
	814773	111	male?
ONYCHOTEUTHIDAE (OEGOPSIDA)			
Onychoteuthis banksii (Leach, 1817)	727524	93	female
OPISTHOTEUTHIDAE (CIRRATA)			
Opisthoteuthis agassizi Verrill, 1883	817405	27	female
O. californiana Berry, 1949	575640	31	female
SEPIIDAE (SEPIOIDEA)			
Sepia officinalis Linné, 1758	817479	84	male
SEPIOLIDAE (SEPIOIDEA)			
Rossia pacifica Berry, 1911	214611	33	female
Sepiola atlantica Orbigny, 1839-1842	575463	16	female
	575463	15	male
SPIRULIDAE (SEPIOIDEA)			
Spirual spirula (Linné, 1758)	814005	42	female
STAUROTEUTHIDAE (CIRRATA)			
Stauroteuthis syrtensis Verrill, 1879	817381	54	female?
	817383	50	not det.
THYSANOTEUTHIDAE (OEGOPSIDA)			
Thysanoteuthis rhombus Troschel, 1857	730192	147	male
VAMPYROTEUTHIDAE (VAMPYROMORPHA)			
Vampyroteuthis infernalis Chun, 1903	885677	55	female

these states were entered. When a character was not applicable to *Nautilus* and fossil/ontogenetic information was lacking, a "?" was entered in the data matrix.

Cladistic analyses were calculated using PAUP, version 3.1.1 (Swofford, 1993) and checked with Hennig86, version 1.5 (Farris, 1988) because the two programs treat data slightly differently in some circumstances (Platnick *et al.*, 1991). All characters were unweighted. In PAUP, a heuristic search was run utilizing the random stepwise addition sequence and the tree bisection-reconnection branch-swapping algorithm. To insure locating the shortest trees, 100 replicates were run, and a strict consensus was performed on all minimum-length trees. Hennig86 analyses used the "ie*" option to utilize all available tree space, and then a Nelsen consensus tree was calculated for the results. When a family was polymorphic for a character, this was entered as a separate state in Hennig86, as opposed to polymorphic coding for PAUP.

The consensus trees were analyzed with MacClade, version 3.0 (Maddison and Maddison, 1992) for impossible character polarization resulting from the use of "?" for unknown or inapplicable characters in the *Nautilus*/ancestral-coleoid taxon. No such cases were found. Information on character transformation was taken from analyses in MacClade. Data on the ingroup and outgroup were analyzed simultaneously and unrooted, then subsequently rooted between the ingroup and outgroup (Nixon and Carpenter, 1993).

RESULTS

CHARACTER DESCRIPTIONS

Character No. 1: Siphuncle. Character states: 0 - absent; 1- present.

Comments. The presence of a siphuncle is well known in *Sepia, Spirula, Nautilus,* and numerous fossil cephalopods and state 1 (present) is clearly the plesiomorphic condition in coleoids. Less well known is the possible remnant of the siphuncle in *Vampyroteuthis*. In *Vampyroteuthis* a long, very slender duct, continuous with the visceropericardial (VP) coelom, extends posteriorly from the coelom to an expanded but flattened sac that sits within the apex of the gladius (Fig. 1A). The posterior wall of the sac is complex histologically on its exterior surface but the function is unknown. The pigmented coelomic epithelial lining makes the thread-like duct visible. Pickford (1940) believed this duct to be a remnant of the siphuncle. The siphuncle of living cephalopods contains an extension of the VP coelom and the duct in *Vampyroteuthis* arises in the position where the siphuncle would be expected (*i. e.* body midline). Alternatively the duct could represent the first stage in the reduction of the coelom leading to the octopod condition. In octopods, narrow ducts, found in other locations, resulted from the reduction of the coelom (*i. e.* the "water canals") (see Character 20). In *Vampyroteuthis* the coelom proper terminates well in advance of the conus of the gladius, a condition not found in decapods. Understanding the structure and function of the "end organ" in *Vampyroteuthis* might help resolve the homology of this duct. For the purposes of this study, we have considered the duct to be homologous with the siphuncle.

Character No. 2: Gladius ostracum. Character states: 0 - present; 1- absent.

Comments. The internal shell of many Recent coleoid cephalopods consists of a thin, chitinous, often feather-shaped structure called the gladius (Figs. 2, 3). Bizikov (1991) considered the gladius to consist of three parts: the periostracum (also known as the rostrum); the ostracum (usually the primary component and often the only obvious component of the gladius), and the hypostracum (a cartilage-like thickening of the gladius apparent in some species). Only the ostracum was considered for this character. The shell (cuttlebone) of sepiids looks very different from a gladius. However, if the calcareous material of this shell is dissolved away, a chitinous structure resembling a broad gladius ostracum remains (along with other separable components) (Fig. 2B). We assume this to be the homologue of the gladius. This is not the case in *Spirula* where only components of the septa and siphuncle remain after dissolution of the calcium carbonate. In some other groups (Sepiolidae, Idiosepiidae) the ostracum is reduced in length but this was not considered as a separate character state at the present level of analysis. The cartilage-like shell of the cirrate octopods is superficially, at least, similar to the "hypostracum" of some teuthoids, and we do not consider this or the stylets (shell remnant of some incirrates) to be "ostraca" in the sense employed here.

Character No. 3: Shell composition. Character states: 0 - calcareous material present; 1 - chitin without calcareous material; 2 - without "typical" chitin or calcareous material (*i.e.* cartilaginous); 3- shell absent.

Comments. In most cases the shell composition in this study was estimated just from the visual appearance of the shell. A white, chalky shell as seen in *Nautilus, Sepia,* and *Spirula* was coded as calcareous; a thin, generally amber shell as seen in teuthoids was coded as chitinous; a thick, translucent structure as seen in cirrate octopods was coded as cartilaginous. Octopod stylets were classified as state 2 rather than as a fourth state. Chemical analysis would probably better define these states.

Character No. 4: Internal shell shape. Character states: 0 - flat and elongate; 1 - U-shaped; 2 - coiled; 3 - stylets; 4 -

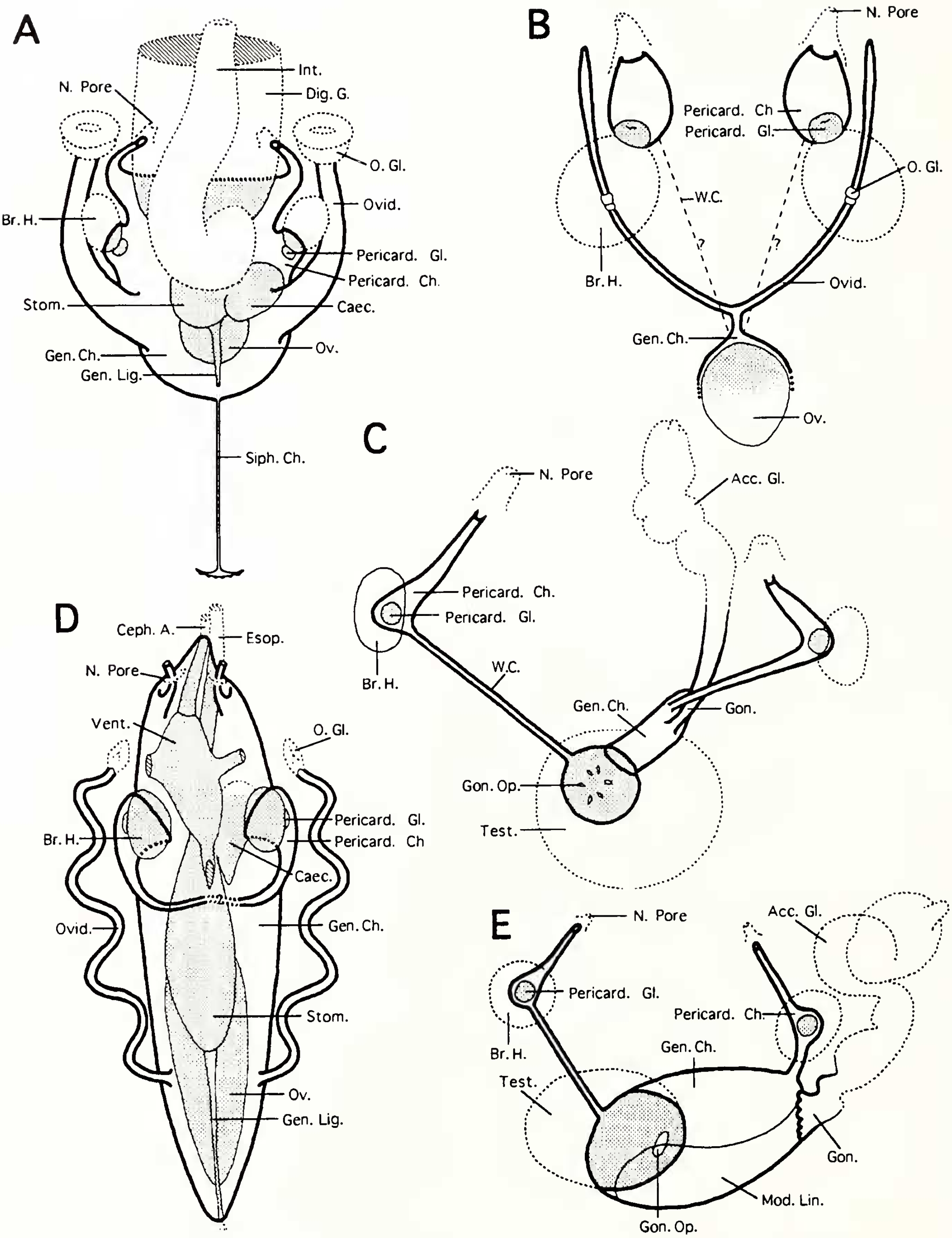

Fig. 1. Visceropericardial coelom. A. *Vampyroteuthis.* B. *Japetella.* C. *Grimpoteuthis.* D. *Sthenoteuthis,* shaded portions of the ink sac, branchial hearts, and intestine are covered by coelomic lining (*i.e.* they "lie" within the coelomic cavity). E. *Stauroteuthis.* (Acc. Gl., accessory gland; Br. H., branchial heart; Caec., caecum; Ceph. A., cephalic artery; Dig. G., digestive gland; Esop., esophagus; Gen. Ch., genital chamber of coelom; Gen. Lig., genital ligament; Gon., gonoduct; Gon. Op., gonadal opening to coelom; Int., intestine; Mod. Lin., modified lining; N. Pore, nephridial pore; O. Gl., oviducal gland; Ov., ovary; Ovid., oviduct; Pericar. Ch., pericardial chamber of coelom; Pericar. Gl., pericardial gland; Siph. Ch., siphuncular chamber of coelom; Stom., stomach; Test., testis; Vent., ventricle; W.C., water canal, thickness exaggerated).

NA (absent).

Comments. This character refers to the general shape of the internal shell. "Elongate" refers to elongation in the direction of the body axis (Fig. 3A). Stylets are elongate but not strictly in the direction of the body axis (Fig. 10B) and are not flattened. NA (not applicable) refers to the loss of an internal shell in some incirrate octopods. Under "U-shaped" we included the various modifications found in cirrate octopods (see Voss, 1988).

Character No. 5: Buccal crown. Character states: 0 - absent; 1 - present as oral arms; 2 - present.

Comments. The buccal crown consists of the muscular buccal supports and the connecting membrane that surrounds the mouth and lips (Fig. 4A). Naef (1928) considered the oral arms (inner ring of tentacles) of *Nautilus* (Fig. 4B) to be homologous with the buccal crown of decapods because of their similar location and because the buccal supports in decapods arise from secondary budding off the arm buds (in Boletzky, 1993b). Also, the buccal supports resemble arms in their possession of suckers in a few families (Fig. 4A). We, therefore, consider the presence of a buccal crown to be plesiomorphic within the Coleoidea.

Character No. 6: Arms II. Character states: 0 - unmodified; 1- filaments; 2 - absent.

Comments. The presence of ten equal arms in early coleoid fossils (*e. g. Jeletzkya*, Middle Pennsylvanian) suggests that the ancestral coleoid had ten equal arms. Naef (1928) noted that in the developing octopod embryo the primary folds from which the eyelids derive lie between arms II and III while in the decapods they lie between arms III and IV suggesting that the missing arm in octopods was one of the first three pairs (in Boletzky, 1993a). Because the first arm rudiment is widely separated from the others only in decapods, he suggested that the first arms were missing in octopods. Boletzky (1978-1979), however, found another marker, the metabrachial vesicles, that lies between arms I and II in both octopods and decapods and suggested that the missing arms are either arms II or III. The filaments in *Vampyroteuthis* lie in the position of a second pair of arms (Fig. 3A). R. E. Young (1967) found that the primary nerve trunks between the filaments and the subesophageal lobes of the brain largely bypassed the brachial lobe and suggested that the filaments might be homologous with the pre-ocular tentacles of *Nautilus*. On the other hand, J. Z. Young (1977) found, by dissection, nerves extending from the filament to each of two ganglia

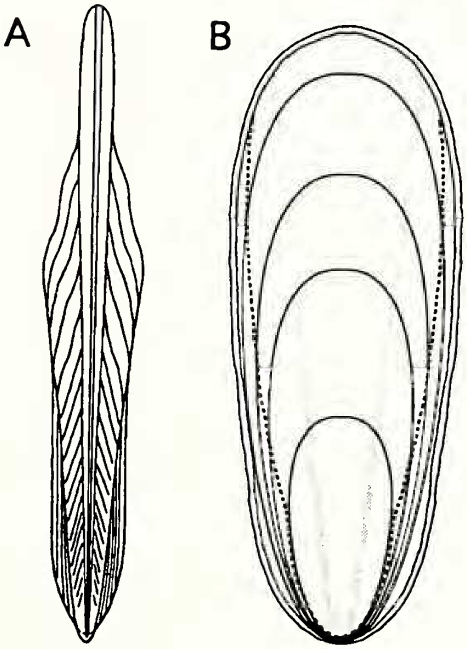

Fig. 2. Gladius ostracum. A. *Abralia*. B. *Sepia*, extracted from cuttlebone by dissolving calcium carbonate in weak acid. Ovals are representative growth lines; oblique lines mark inner margins of thickened layers on the ventral surface of the ostracum.

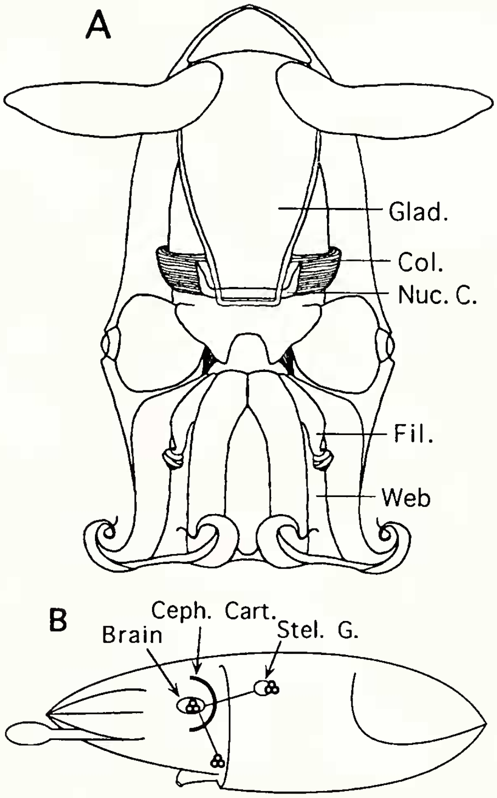

Fig. 3. A. Diagrammatic illustration of *Vampyroteuthis* showing position of the filaments, nuchal cartilage and gladius (modified after R. E. Young, 1962). B. Generalized cephalopod showing positions occupied by photosensitive vesicles. (Ceph. Cart., cephalic cartilage; Col., collar muscle; Fil., filament; Glad., gladius; Nuc. C., nuchal cartilage; Stel. G., stellate ganglion).

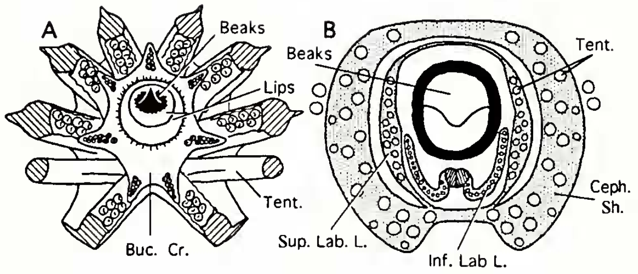

Fig. 4. Oral view of arm crowns (diagrammatic). A. *Loligo* (after Naef, 1921-1923) showing armature of arms in two series and suckers on the buccal crown. B. *Nautilus* (modified after Griffin, 1900). (Buc. Cr., buccal crown; Ceph. Sh., cephalic sheath; Inf. Lab. L., inferior labial lobe bearing tentacles; Sup. Lab. L., superior labial lobe bearing tentacles; Tent., tentacle).

on the circumoral commissure (= nerve ring). The latter connects the axial nerves of all the arms. He considered this proof that the filaments were modified arms II. We have made several attempts to confirm the existence of these connecting nerves to the filaments but failed to find them. Numerous small nerves radiate from the ganglia on the circumoral commissure to various muscles. In addition, the region is crossed by numerous slender muscle or connective tissue fibers. As a result, the nervous connections could be easily misinterpreted. The possible absence of a connecting nerve again opens the question of the homology of the filaments but does not disprove their origin from the second pair of arms. Indeed, the axial nerve of the tentacles (fourth arms) of some decapods (*e. g. Loligo, Sepia*) does not have a connection with the circumoral ring (Fig. 5B).

For this study, character coding was based on the assumptions that (1) the octopods have lost arms II, and that (2) the vampire filaments are modified arms II. Under these assumptions, the character states can be analyzed as "ordered": unmodified - filaments - absent.

Character No. 7: Arms IV. Character states: 0 - unmodified; 1 - tentacles.
Comments. Decapods retain the ten arms of the ancestral coleoid but arms IV have been modified into tentacles (Fig. 4A).

Character No. 8: Sucker rings. Character states: 0 - cuticular rings; 1 - no rings; 2 - horny rings.
Comments. This character refers to the secreted linings of suckers. The cuticular lining in octopods is chitinous (Hunt

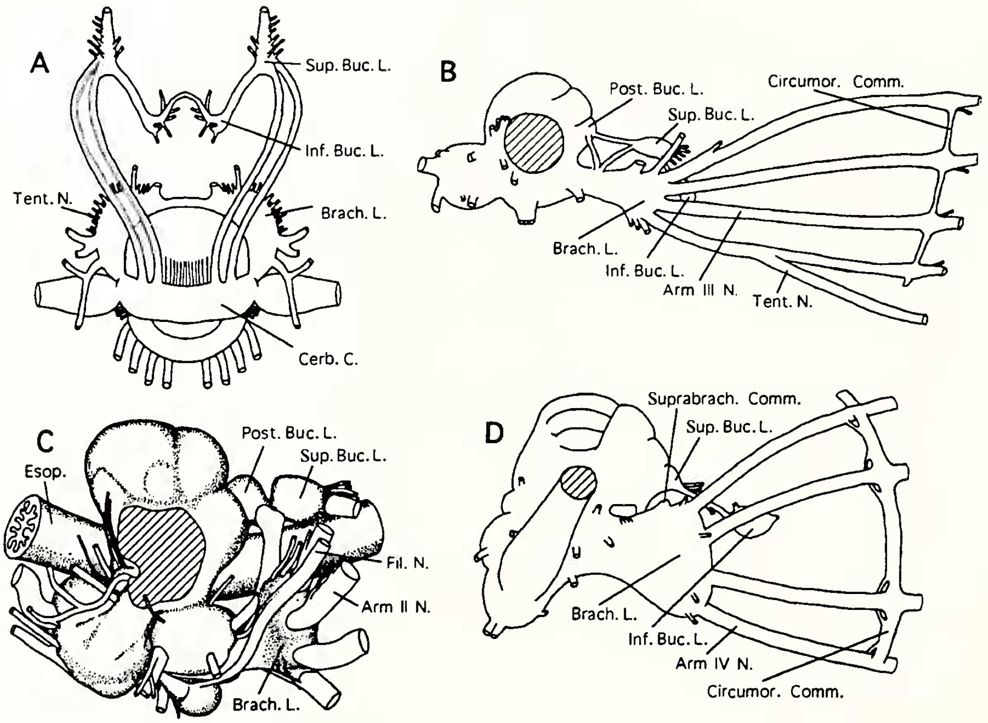

Fig. 5. Central nervous system (brain). A. *Nautilus* (modified after Griffin, 1900). B. *Sepia* (modified after Hillig, 1913). C. *Vampyroteuthis* (modified after R. E. Young, 1967). D. *Octopus* (modified after J. Z. Young, 1971). Arm numbering between taxa is based on morphological position not necessarily homology. (Arm II N., arm II axial nerve; Arm III N., arm III axial nerve; Arm IV N., arm IV axial nerve; Brach. L., brachial lobe; Cerb. C., cerebral cord; Circumor. Comm., circumoral commissure; Esop., esophagus; Fil. N., filament axial nerve; Inf. Buc. L., inferior buccal lobe; Post. Buc. L., posterior buccal lobe; Sup. Buc. L., superior buccal lobe; Suprabrach. Comm., suprabrachial commissure; Tent. N., tentacle nerve).

and Nixon, 1981). The inner "chitinous" sucker rings found in decapods are thick, generally bear teeth, and are more properly termed "horny" rings because they do not contain chitin (at least in *Sepia*; Rudall, 1955). Otherwise, the chemical composition of the decapod rings is unknown (Nixon and Dilly, 1977). Nixon found no trace of a cuticular lining in *Vampyroteuthis* and our sections confirm her observations. Neither we nor Nixon, however, had suckers in perfect condition.

Character No. 9: Sucker stalks. Character states: 0 - base and neck; 1 - base and plug; 2 - cylinder.
Comments. In octopods, a sucker stalk consists of a broad cylinder of muscles that attaches to the outer lateral walls of the acetabulum often at the point where the latter joins the infundibulum (Fig. 6A). Also, oblique muscle fibers cross within the cylinder (Graziadei, 1971). In decapods, a sucker stalk consists of a broad conical base that tapers gradually or abruptly to a neck of varying length (Fig. 6B). The neck is a narrow muscular rod that attaches off-center within the base of the sucker acetabulum. Superficially the sucker stalks in *Vampyroteuthis* resemble those of the decapods in having a broad base and a short neck (Fig. 6C). Both components, however, differ substantially from the decapod condition. The neck attaches (virtually adhears) to the connective tissue at the base of the acetabulum. In decapods the neck muscles and other tissues invade and form part of the acetabulum. The base in *Vampryoteuthis* does not clearly attach as a unit to the arm muscles. The major attachment is a band of muscles that runs proximally from the sucker neck, along the midline of the arm, to attach to the arm muscles beneath the base of the preceeding sucker. The relationships of the peculiar sucker stalk of *Vampyroteuthis* to that of the decapods and octopods is not clear at present and we have considered it a separate character state.

Character No. 10: Sucker symmetry. Character states: 0 - radial symmetry; 1 - bilateral symmetry.
Comments. The sucker is radially symmetrical in *Vampyroteuthis* and the octopods but strongly bilateral in the decapods (Fig. 6). The bilaterality of the latter is most apparent in the shape of the horny rings and the point of attachment to the stalk.

Character No. 11: Arm III armature series. Character states: 0 - one; 1 - two; 2 - four; 3 - more than four.
Comments. "Armature series" refers to the number of sucker and/or hook series paralleling the arm axis in the midportion of the arm (Fig. 4A). We restricted the character to the arm midportion as the armature series often differs at the tips and bases of the arms. In incirrate octopods, suckers almost invariably begin in embryos as a single series regardless of the number of series in the adults (Naef, 1921-1923). This suggests that a single series is plesiomorphic in the Octopoda. In decapods, hatchlings of many species have two or more rows and the plesiomorphic state is uncertain. *Nautilus* has a series of rings encircling the arms that can form a suction on their oral surfaces. This could be interpreted as a precursor to a single sucker series in early coleoids. This possibility, however, is contradicted by the presence of two rows of hooks in one of the oldest coleoids (*Jeletzkya*).

Character No. 12: Arm V sucker series. Character states: 0 - one; 1- two; 2 - four; 3 - more than four.
Comments. Armature series on arms V is not always the same as on arms III. As a result we regarded this as a separate character. As above the armature series refers to that in midarm.

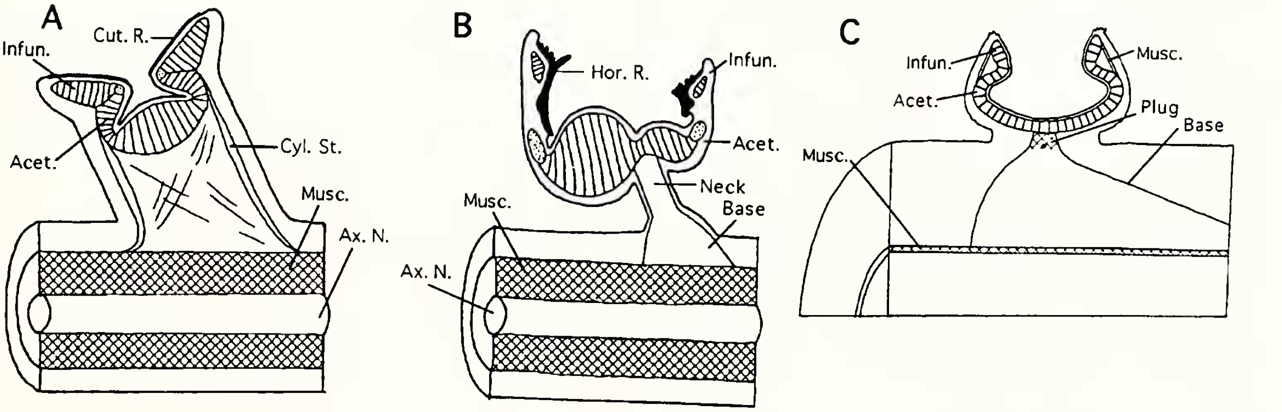

Fig. 6. Longitudinal sections of suckers (diagrammatic). A. *Octopus* (modified after Naef, 1921-1923). B. *Loligo* (modified after Naef, 1921-1923). C. *Vampyroteuthis*. (Acet., acetabulum; Ax. N., axial nerve; Cut. R., cuticular ring; Cyl. St., cylindrical stalk; Hor. R., horny ring; Infun., infundibulum; Musc., muscle).

Character No. 13: Trabeculae on unmodified arms. Character states: 0 - present; 1 - absent.
Comments. "Unmodified" refers to arms not modified for sexual functions. Trabeculae, in their most recognizable form, are conical, muscular structures that arise lateral to the suckers on the arms and are attached to the muscular cylinder of an arm. In some cases the identification of trabeculae is difficult without sectioning. Our character states were coded on the basis of general appearance and not histological sections. We, therefore, defined trabeculae as "present" only when they were clearly recognizable from their associated membranes. Therefore, if trabeculae are present but obscure, they will be incorrectly coded as absent. When membranes are lacking, possible trabeculae can be confused with skin folds associated with sucker bases. In this case, a distinct muscular pillar must be recognized to qualify as a trabecula. Trabeculae are not to be confused with the muscular sucker bases with which they are often associated. The origin of trabeculae is uncertain but they are similar in structure to sucker bases and, indeed, in a variety of cephalopods sucker bases are modified into structures apparently identical with trabeculae (*e. g.* on hectocotylized arms in a variety of squids, on the distal tips of the arms in *Vampyroteuthis*). Although the trabeculae are modified in a variety of ways in decapods, in many (*e. g. Thysanoteuthis*) the basic structure and attachment are identical to the cirri of octopods. Naef (1921-1923) considered trabeculae and cirri to be homologues and they were treated so in this study.

Character No. 14: Protective membranes on unmodified arms. Character states: 0 - absent; 1 - present.
Comments. "Unmodified" refers to arms not modified for sexual functions. An arm protective membrane is a membrane that connects trabeculae and lies lateral to the suckers/hooks. When trabeculae cannot be clearly recognized, the definition changes to: a membrane that is uninterrupted, at least along its free margin, by sucker bases. The octopod, *Ocythoe*, for example has membranes that are completely interrupted by suckers (*i. e.* the membrane extends from sucker to sucker) and, therefore do not qualify as "protective membranes" as defined here. To code this character as present, membranes need be present only on a portion of an arm, *e. g. Vampyroteuthis* which has protective membranes only near the arm tips (Pickford, 1946). There is no relevant character state for *Nautilus*.

Character No. 15: Well-developed interbrachial web between arms I. Character states: 0 - virtually absent; 1 - present.
Comments. "Well-developed" means the center of the web extends more than 20% of the arm length measured from the point where adjacent arms join (Fig. 3A). The sector between arms I was picked because this sector often has the lowest web development among the dorsal arms. Coding of this character was somewhat subjective in a few cases.

Character No. 16: Well-developed interbrachial web between arms V. Character states: 0 - absent; 1 - present.
Comments. "Well-developed" means the center of the web extends more than 20% of the arm length. The sector between arms V was picked because this sector generally has the lowest web development among the ventral arms. The absence of a web between arms V is often independent of the web condition of the dorsal arms. *Nautilus* lacks a relevant character state.

Character No. 17: Fin cartilage. Character states: 0 - at proximal end of fin; 2 - at proximal end and in core; 3 - NA (fins absent).
Comments. In decapods the fins typically insert on a flattened cartilage with a slight medial ridge; the cartilage attaches to the shell sac. In cirrates the fin cartilage has generally been considered to be absent (Robson, 1932). In *Vampyroteuthis* the problem of comparison is complicated by the fact that this animal has two pairs of fins. The juvenile fin appears first and the adult fin later in a more anterior position; with growth the juvenile fins are resorbed and the adult fins enlarge (Pickford, 1950). In dissecting and sectioning the fins of cirrates, we found that they have a fin cartilage with a small "base" that adheres to the shell sac and an extensive "plate" that occupies the core of the proximal half of the fin (Figs. 7A-D). The cartilage consists of a highly vacuolated tissue with virtually no matrix other than the thin walls of the vacuoles. The flexible, spongy consistency is apparently responsible for it not being previously recognized as cartilage. The adult vampire fin has a small cartilage at the tip of the attached end of the fin and the fin has an L-shape that is very different from those of cirrates or decapods (Figs. 7E, F). The juvenile fin of *Vampyroteuthis* has an internal cartilage similar to that of the cirrates but with a much larger flattened, cartilaginous "base" attached to the shell sac and a slender cartilaginous "plate" (continuous with the base) that extends through the entire core of the fin (Figs. 7G, H). The histology is the same as in the cirrates except that the vesicles are larger in *Vampyroteuthis* (Fig. 7I). We consider the juvenile fin of *Vampyroteuthis* to be the homologue of the octopod and decapod fins.

The absence of fins in incirrates is clearly secondary as their anlagen are present in the embryo but disappear during development (Naef, 1921-1923).

Character No. 18: Statocyst outer capsule. Character states: 0 - outer capsule absent; 1 - outer capsule present.
Comments. Statocysts have one of two basic structures in

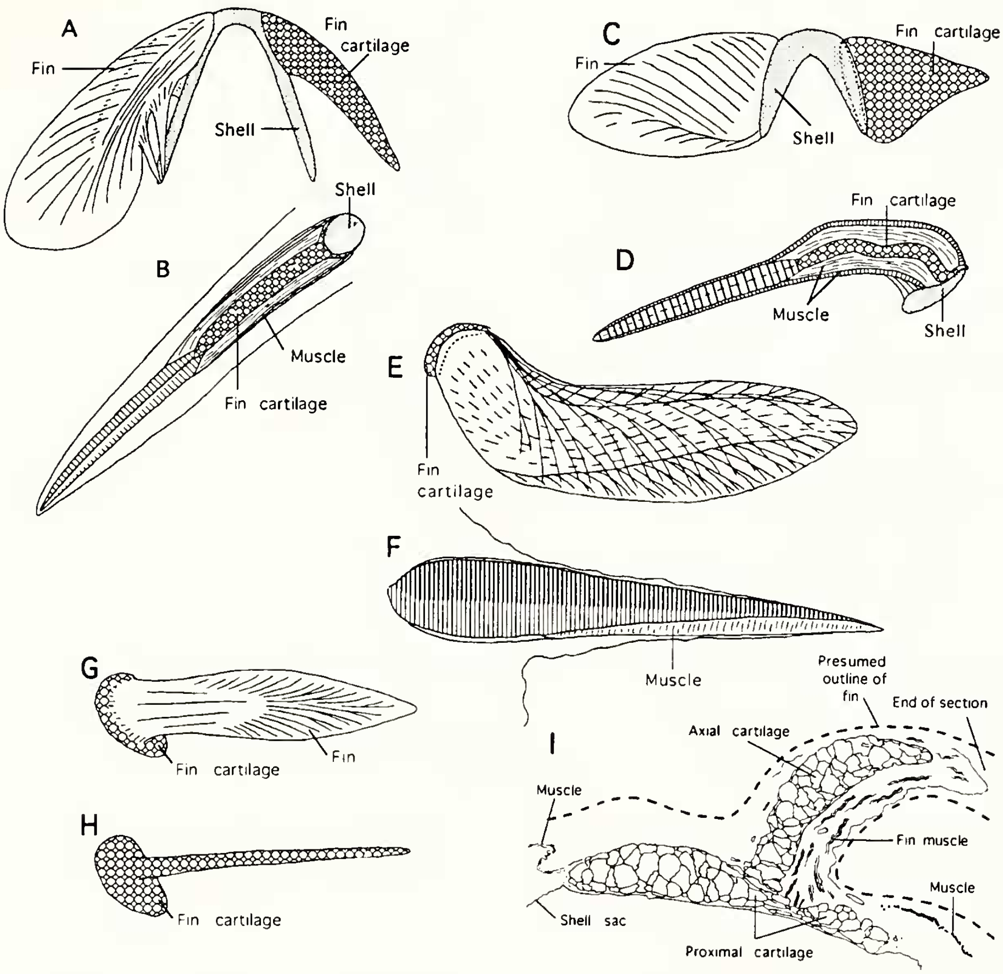

Fig. 7. Fins (diagrammatic). A. *Grimpoteuthis*, ventral view with outer tissue removed. B. *Grimpoteuthis*, longitudinal section through fin. C. *Stauroteuthis*, ventral view with outer tissue removed. D. *Stauroteuthis*, longitudial section through fin. E. *Vampyroteuthis*, adult fin, dorsal view. F. *Vampyroteuthis*, adult fin, longitudinal section through straight portion of fin. G. *Vampyroteuthis*, juvenile (= "larval") fin, dorsal view. H. *Vampyroteuthis*, juvenile fin, dorsal view with outer tissue removed. I. *Vampyroteuthis*, longitudinal section through juvenile fin.

cephalopods: they consist of a single sac that is commonly embedded directly in cartilage or they lie within an additional fluid-filled sac, the outer capsule, which is commonly embedded in cartilage.

Character No. 19: Nephridial coelom. Character states: 0 - nephridial coeloms separate (unipaired); 1 - nephridial coeloms fused (single coelom).
Comments. In *Vampyroteuthis infernalis*, left and right nephridial sacs are separated from one another by their medial walls (Fig. 8A) and further by the intestine which lies between the medial walls at their ventral ends (Fig. 8B). Each has a rather simple shape and includes renal appendages arising from (1) the cephalic vein, (2) vena cava en route to the branchial heart, and (3) a dorsal branch of the vena cava (the latter forms an abbreviated dorsal lobe).

In the incirrate *Japetella diaphana* the left and right nephridial sacs are, also, entirely separate and a more distinct dorsal lobe is present (Figs. 8C, D).

The nephridial coelom has not been well described in the teuthoids. In dissecting *Sthenoteuthis oualaniensis* (Lesson, 1830) we found the coelom divided into two chambers: the dorsal and ventral sacs (Figs. 8E, F). The ventral sac is roughly Y-shaped with the stem of the Y directed anteriorly and the arms defined by a septum that partially divides the cavity posteriorly. The cephalic vein enters the cavity dorsally. The renal appendages are restricted to the ventral sac although the cephalic vein has what seems to be tiny appendages near its dorsal entrance. The ventral sacs surround the intestine, ink sac, and the extensive lobes of the digestive gland duct appendages (DGDA) (see Character 43). Communication between the dorsal and ventral sacs occurs to either side of the inflated

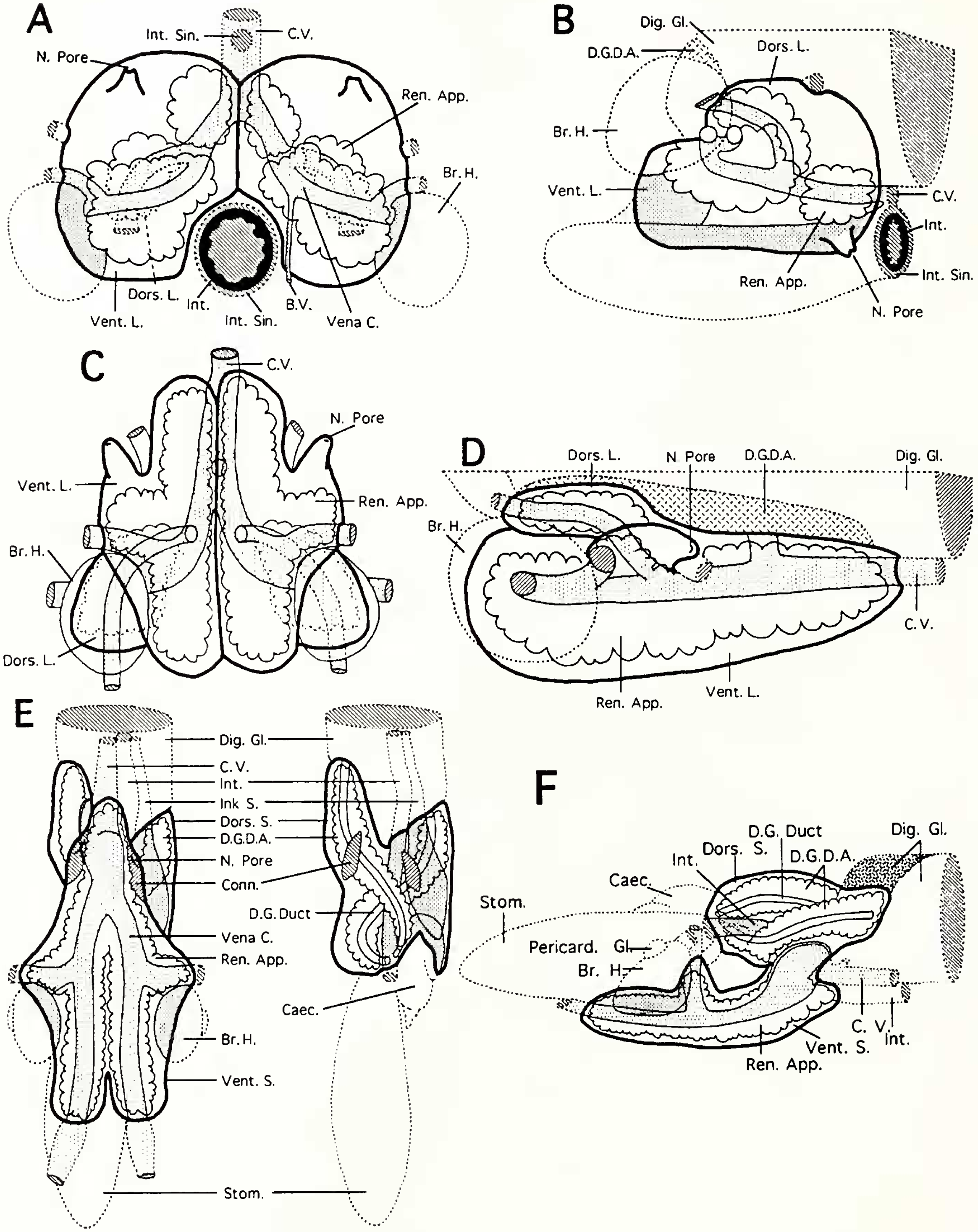

Fig. 8. Nephridial coelom (diagrammatic). A. *Vampyroteuthis*, ventral view. B. *Vampyroteuthis*, side view. C. *Japetella*, ventral view. D. *Japetella*, side view. E. *Sthenoteuthis*, left: ventral view; right: ventral view with ventral sac removed. F. *Sthenoteuthis*, side view. (B. V., blood vessel; Br. H., branchial heart; Caec., caecum; Conn., connection between dorsal and ventral sacs of coelom; C. V., cephalic vein; D. G. D. A., digestive gland duct appendages; D. G.Duct, digestive gland duct; Dig. G., digestive gland; Dors. L., dorsal lobe of coelom; Dors. S., dorsal sac of coelom; Ink S., ink sac; Int., intestine; Int. Sin., intestinal sinus; N. Pore, nephridial pore; Pericard. G., pericardial gland; Ren. App., renal appendages; Stom., stomach; Vena C., vena cava; Vent. L., ventral lobe of coelom; Vent. S., ventral sac of coelom).

cephalic vein as it enters the ventral sac. This is generally the same as in *Sepia* (Tompsett, 1939).

In the cirrate *Grimpoteuthis glacialis* (Robson, 1930) the nephridial sacs are also paired (Fig. 9A). Each sac has a very extensive dorsal lobe. The right sac has a dorsal branch that extends posteriorly as a large sac that circles the gonad to its posterior tip and contains renal appendages throughout most of its course. The dorsal branch of the left sac also has a posterior extension but it is very broad and lacks renal appendages although they are present dorsally.

In the cirrate *Stauroteuthis syrtensis* the nephridial sacs are paired as well (Fig. 9B). The dorsal branch off the vena cava is longer than in *Japetella* and carries the bulk of the renal appendages. The dorsal lobe, therefore, is large but its full extent was not mapped.

This character can be difficult to evaluate in preserved specimens. In general if the renal appendages had a Y-shaped morphology along their ventral face (*i. e.* renal appendages begin on the cephalic vein), we assumed that the coelom of either side was continuous (fused) medially.

Character No. 20: Visceropericardial coelom. Character states: 0 - extensive coelom (surrounds visceral nucleus, ventricle and gonad); 1 - coelom reduced (viscera excluded except part of the gonad).

Comments. We have illustrated the visceropericardial (VP) coelom of several species which have not been illustrated previously. The VP coelom of *Vampyroteuthis* (Fig. 1A) surrounds most of the visceral nucleus, much of the posterior end of the digestive gland including part of the digestive gland duct appendages (but see Character 43), posterior end of the crop, ventricle, and the gonad which is suspended in the coelom from the genital strand. The pericardial chamber is represented by short outpocketings on either side of the coelom that enclose the pericardial glands and the medial portions of each branchial heart. At its antero-lateral corners the coelom narrows into ducts that open into the nephridial coelom at the base of the nephridial papillae.

In *Japetella diaphana* the VP coelom (Fig. 1B) is very restricted in extent as appears typical of the incirrate octopods (see Isgrove, 1909). We were, however, unable to locate the water canals but they could have been missed. The degree to which the gonad lies in the coelom could not be fully evaluated as the tissue layers did not separate cleanly. However, the ventral half of the gonad and part of the anterior portion appeared to be within the coelomic cavity.

In *Grimpoteuthis glacialis* the VP coelom is very restricted but less so than in *Japetella* (Fig. 1C). It covers just a small patch of the gonad (here the gonad opens into the coelom). This portion is separated from the rest of the coelomic sac (the outer sac) by a transverse membrane that partially occludes the connection. The gonoduct and the left water canal open into the outer sac near its lateral extent and the right water canal opens into the inner sac. Both water canals extend to a small sac covering the pericardial gland. Anterior ducts from the latter sacs open into the nephridial coelom at the base of the nephridial papillae. There appears to be no genital pocket in the male.

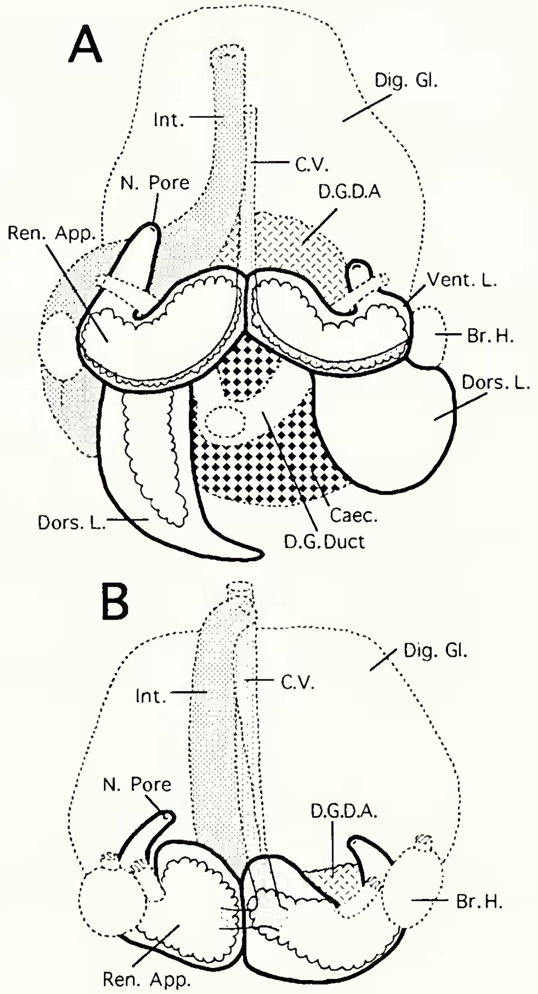

Fig. 9. Nephridial coelom (ventral view, diagrammatic). A. *Grimpoteuthis*. B. *Stauroteuthis*. (Br. H., branchial heart; C. V., cephalic vein; Caec., caecum; D. G. D. A., digestive gland duct appendages; D. G. Duct, digestive gland duct; Dig. G., digestive gland; Dors. L., dorsal lobe of coelom; Int., intestine; N. Pore, nephridial pore; Ren. App., renal appendages; Vent. L., ventral lobe of coelom).

The VP coelom of *Sthenoteuthis oualaniensis* is generally representative of the decapods (Fig. 1D). It extends from the digestive gland to the conus of the gladius and incorporates most of the visceral nucleus (stomach and caecum), ventricle, posterior esophagus, and the gonad. The pericardial chamber of the VP coelom consists of a shelf on the ventral surface of the coelom and encloses much of the branchial hearts and pericardial glands and appears to be continuous across the ventral midline although we could not be certain of this. Anteriorly the VP coelom narrows abruptly into ducts which extend through the nephridial pores to open into the mantle cavity. The extension of the ducts into the mantle cavity could be a peculiarity of this species.

In *Stauroteuthis syrtensis*, the VP coelom is less restricted than in *Grimpoteuthis* and is reduced mostly to a sac that covers, at its right end, a portion of the gonad and leads, at its left end, into the large fluted end of the broad male gonoduct (Fig. 1E). Two narrow ducts ("water canals") extend from the coelomic sac to include the pericardial glands. The right duct is long and slender and the left one short and somewhat broader (the thickness of both is exaggerated in the illustration). From the sac around the pericardial gland a broader and more muscular duct opens into the nephridial coelom at the base of the nephridial papilla on either side. There appears to be no genital pocket in the male.

In *Nautilus*, the VP coelom is extensive and divided into pericardial, genital, and siphuncular chambers. The gonad, part of the intestine, stomach, digestive gland, and ventricle are covered by coelomic epithelium (Griffin, 1900).

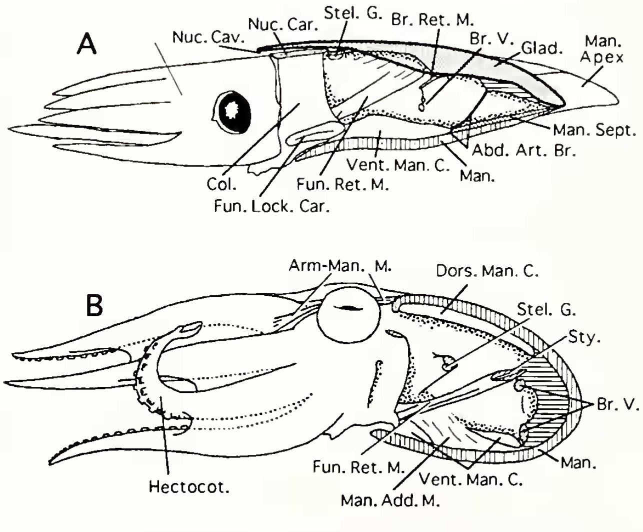

Fig. 10. The teuthoid *Abralia* showing the mantle septum, nuchal cartilage, nuchal cavity, funnel-locking cartilage, and position of stellate ganglion. Heavy line outlines gladius. B. An incirrate octopodid showing the dorsal mantle cavity, position of stellate ganglion, muscle connection between arm bases and anterior mantle margin, mantle adductor muscle, stylets, and hectocotylus. [Abd. Art. Br., abdominal (median pallial) artery and branch (lateral pallial artery); Arm-Man. M., arm-mantle muscle; Br. Ret. M., branchial retractor muscle; Br. V., branchial blood vessel; Col., collar; Dors. Man. C., dorsal mantle cavity; Fun. Lock. Car., funnel locking cartilage; Fun. Ret. M., funnel retractor muscle; Glad., gladius; Hectocot., hectocotylus; Man., mantle; Man. Add. M., mantle adductor muscle; Man. Apex, mantle apex; Man. Sept., mantle septum; Nuc. Car., nuchal cartilage; Nuc. Cav., nuchal cavity; Stel. G., stellate ganglion; Sty., stylet; Vent. Man. C., ventral mantle cavity].

Character No. 21: Dorsal mantle cavity. Character states: 0 - absent; 1 - present.
Comments. This cavity is a dorsal continuation of the ventral mantle cavity, across the dorsal midline, posterior to the stellate ganglia (Fig. 10B). The large dorsal cavity of *Spirula* is excluded from state 1 by its presence anterior to the stellate ganglia and we consider it to be a "nuchal" cavity. Because *Nautilus* lacks stellate ganglia, we define the dorsal mantle cavity, in this case, as a cavity well posterior to the level of the collar. The cavity in the collar region, the "nuchal" cavity, is characteristic of most cephalopods in which the mantle and head are not fused (Fig. 10A). The dorsal mantle cavity as defined here proved to be characteristic of the octopods.

Character No. 22: Nidamental glands. Character states: 0 - absent; 1 - present.
Comments. Nidamental glands of decapods are large, paired organs that open directly into the mantle cavity and are composed of numerous lamellae that are involved in secretion of egg cases or masses. *Nautilus* has a three-lobed, lamellar nidamental gland.

Character No. 23: Crop. Character states: 0 - present; 1 - absent.
Comments. The crop is an expansion or a diverticulum of the esophagus for food storage. For this study, we consider a crop to be absent unless it is morphologically obvious. The cirrate octopods we examined have an esophagus that is only slightly expanded and we considered this as state 1. Others (see Robson, 1932) have indicated the presence of a reduced crop in cirrates which could simply reflect differences in how a crop is defined. These statements, nevertheless, have resulted in our coding the cirrates as polymorphic for this character.

Character No. 24: Branchial canal. Character states: 0 - absent; 1 - present.
Comments. The branchial canal is a large opening at the base of each gill lamella and between the primary afferent and efferent blood vessels of the gill (Figs. 11A, D, E). This canal allows passage of sea water between lamellae at this point. This unambiguous character was a primary feature used by systematists for many years to separate teuthoids from sepioids.

Character No. 25: Mantle septum. Character states: 0 - absent; 1 - present and continuous; 2 - present but open posteriorly; 3 - blood vessel only.

Comments. The mantle septum passes from the ventral surface of the visceral mass, across the mantle cavity to the inner surface of the mantle wall (Fig. 10A). The membrane lies in an anterior/posterior orientation and divides the mantle cavity into right and left sides. Along its anterior margin, the membrane supports, in decapods, a branch of the abdominal aorta as it passes from the visceral mass to the ventral mantle wall. Character state 3 occurs only in *Spirula* where the coiled shell leaves room for only the artery. No septum is present in *Nautilus*; however, the very different organization of the mantle cavity suggests that this character is not applicable to *Nautilus.*

Character No. 26: Mantle adductor. Character states: 0 - absent; 1 - present; 2 - NA.
Comments. The mantle septum commonly has slender muscle fibers running along it primarily in an anterior-posterior direction. In some cephalopods, a pronounced muscle bundle, the mantle adductor, is present that runs more or less ventrally from the visceral mass to the mantle wall (Fig. 10B). Presumably an adductor cannot exist without a mantle septum as a precursor. NA refers to the absence of the mantle septum. *Nautilus* lacks a relevant character state.

Character No. 27: Funnel valve. Character states: 0 - present; 1 - absent.
Comments. The funnel valve is a muscular flap, continuous with the postero-dorsal wall of the funnel, that lies within the lumen of the funnel.

Character No. 28: Nuchal cartilage. Character states: 0 - present; 1 - absent.
Comments. The nuchal cartilage is the support for the head component of the nuchal locking apparatus (Fig. 10A). Muscles of the collar and muscles from the head and shell sac attach to this cartilage. In *Vampyroteuthis*, although the head and mantle are fused, a nuchal cartilage remains (Fig. 3A). Its shape varies from a flat rectangle to a low U-shape and lies beneath and just posterior to the anterior end of the cartilage that surrounds much of the periphery of the gladius. The cartilage no longer supports a locking apparatus but still provides a site for muscle attachment. *Nautilus* lacks a mantle-propulsion system which, presumably, is a prerequisite for development of a nuchal cartilage; it has no relevant character state.

Character No. 29: Cornea. Character states: 0 - cornea absent; 1 - one-part cornea present; 2 - two part cornea present.
Comments. The cornea is a transparent, protective covering of the lens. Here we consider all one-part corneas as homologues; although this is a debatable assumption it is not critical at this level of analysis. *Nautilus* lacks a relevant character state because its eyes do not bear lenses.

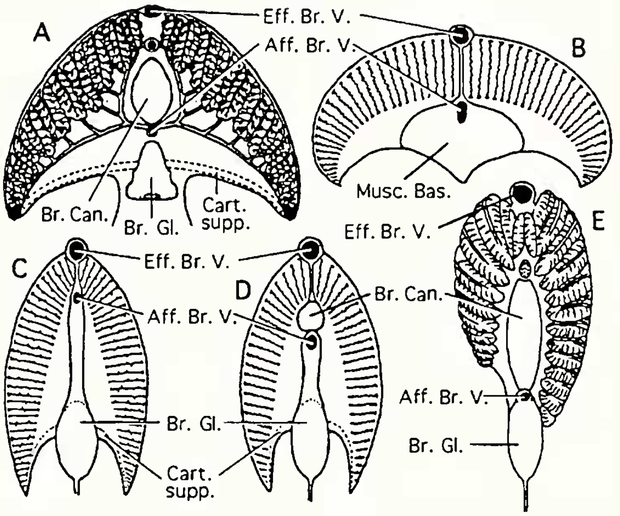

Fig. 11. Gill filaments (diagramatic). A. *Vampyroteuthis* (modified after R. E. Young, 1962); B. *Nautilus* (modified after Naef, 1921-1923); C. *Sepia* (modified after Naef, 1921-1923); D. *Loligo* (modified after Naef, 1921-1923); E. Incirrate octopod (modified after Naef, 1921-1923). (Aff. Br. V., afferent branchial vessel; Br. Can., branchial canal; Br. Gl., branchial gland; Cart. supp., cartilagenous supporting rod; Br. Gl., branchial gland; Eff. Br. V., efferent branchial vessel; Musc. Bas., muscular base).

Character No. 30: Right oviduct. Character states: 0 - absent; 1 - present.
Comments. The oviducts are gonoducts that open into the visceropericardial coelom and exit into the mantle cavity (Figs. 1A, B, D). In coleoids the left, but not the right, oviduct is always present. "Present" refers to physical presence irrespective of functionality.

Character No. 31: Oviducal gland symmetry. Character states: 0 - radial symmetry; 1 - bilateral symmetry; 2 - asymmetry.
Comments. The oviducal glands are organs that surround the oviducts and contain numerous glandular lamellae that are involved in secretion of egg cases or masses. The oviducal gland of *Vampyroteuthis* surrounds the oviducal opening and consists of two thick, contiguous, equal-sized rings. Each ring is composed of flattened lamellae. Typically the leaflets of the outer ring which are attached only proximally are freely exposed to the mantle cavity. A circular membrane that covers the more proximal ring, however, is capable of expanding to cover the outer ring. The entire organ is radially symmetrical (Fig. 12B). The double nature of the gland is characteristic of coleoids. In decapods the proximal portion is much smaller and both proximal and distal portions are bilaterally symmetrical (Fig. 12C) while in octopods the distal portion is often smaller and the glands

are radially symmetrical. The oviducal gland of *Nautilus* forms the terminal portion of the oviduct. It appears to be highly glandular and has thick folds or lamellae. The gland, in our poorly preserved specimens, has a slit-like opening and the arrangement of lamellae shows it to be asymmetrical (Fig. 12A).

Character No. 32: Oviducal gland position. Character states: 0 - gland terminal (located at end of oviduct); 1 - gland subterminal (oviduct continues distal to gland).
Comments. Oviducal glands are located either at the opening of the oviduct (Figs. 1A, D) or well proximal to the oviduct external opening which thereby defines a distinct distal oviduct (Fig. 1B). A distal oviduct can be identified by the lack of glandular leaflets and often lacks a circular orifice. In *Sepiola* the distal portion of the oviducal gland is very slender and elongate and gives the false impression of a distal oviduct.

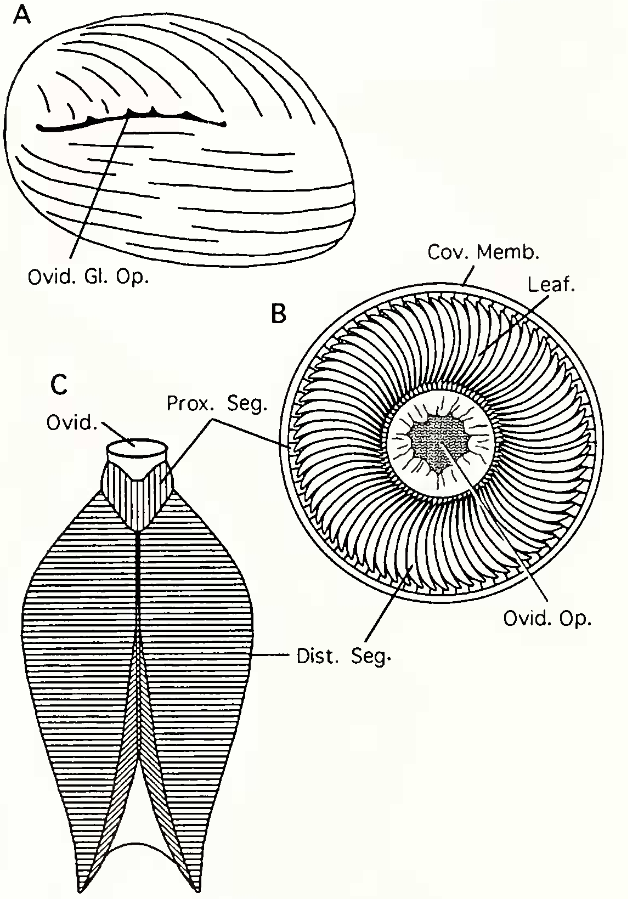

Fig. 12. Oviducal glands (diagramatic). A. *Nautilus*. B. *Vampyroteuthis*. C. *Abralia*. (Cov. Memb., covering membrane; Dist. Seg., distal segment of oviducal gland; Leaf., leaflet; Ovid., oviduct; Ovid. Gl. Op., oviducal gland opening; Ovid. Op., oviduct opening; Prox. Seg., proximal segment of oviducal gland).

Character No. 33: Photosensitive vesicles. Character states: 0 - within cephalic cartilage; 1 - above funnel; 2 - on stellate ganglia.
Comments. The photosensitive vesicles are vesicular organs that function in detection of light for a variety of purposes. In decapods they occupy a variety of locations but all are within the region of the head bounded by the cephalic cartilage (Fig. 3B). In octopods they lie on the stellate ganglia and in *Vampyroteuthis* they lie just above the dorsal surface of the funnel (Fig. 3B). Photosensitive vesicles have never been described in *Nautilus*. This is an unambiguous character that has been previously described in most families of concern here.

Character No. 34: Inferior frontal lobe system of the brain. Character states: 0 - absent; 1 - partially present; 2 - present.
Comments. The inferior frontal lobe system of octopods consists of the inferior frontal, subfrontal, and posterior buccal lobes (J. Z. Young, 1971). In decapods this entire system is represented by the posterior buccal lobes (often called the inferior frontal lobes) (J. Z. Young, 1988). In *Vampyroteuthis* the complex connections posteriorly from the posterior buccal lobe (*sensu lato*) and the central region of the supraesophageal mass is much more complex than in decapods and J. Z. Young (1977: 385) suggested it "may represent a poorly differentiated subfrontal lobe." He considered this and some differentiation of the dorsal part of the buccal lobe which he interpreted as an inferior frontal lobe, to be a stage of "incipient development of an apparatus for more elaborate processing of tactile information... ." We agree with this interpretation and coded this character as a separate state for *Vampyroteuthis* that is intermediate between the octopod and decapod conditions. This transformation series is best defined as "ordered." The construction of the brain of *Nautilus* is very different from coleoids and cannot be coded for this character.

Character No. 35: Head-mantle fusion: arm-base-to-anterior-mantle muscle. Character states: 0 - present; 1 - absent.
Comments. In a variety of coleoids the dorsal surface of the mantle has become fused to the head. The variation in the details of the fusion indicate that fusion has occurred several times during evolution. Character 35 describes a characteristic of the octopod fusion in which muscles attach at the junction of the dorsal arm bases and on the anterior edge of the dorsal mantle (Fig. 10B). As a result, it lumps all other families together under state 1 (absent). This is acceptable at our present level of analysis because state 1 is the plesiomorphic state in the Coleoidea. Even though *Nautilus* lacks a mantle-propulsion system, we consider its

lack of head-mantle fusion a relevant state.

Character No. 36: Arm III hectocotylization. Character states: 0 - absent; 1 - present.
Comments. Hectocotylization refers to the modification of an arm in males for the transfer of sperm to the female (Fig. 10B). Arm III in octopods and vampyromorphs could be the homologue of arm IV (tentacle) in decapods (see Character 6). For this character we have not made this assumption and compared the morphological arm III in all groups. The distribution of this character, however, would be the same for either interpretation of arm relationships. Either one or both members of an arm pair could be modified. Because *Nautilus* lacks specific homologues to each of the ten arms of coleoids, it has no relevant character state.

Character No. 37: Arm V hectocotylization. Character states: 0 - absent; 1 - present.
Comments. We assume that the hectocotylization of different arm pairs (cf. Character 36) represents independent evolutionary events and, therefore, qualify as separate characters.

Character No. 38: Collagenous tunics on mantle. Character states: 0 - absent; 1 - present.
Comments. Many decapods contain a collagenous tunic over the mantle that, apparently, acts to resist change in mantle length during the jet cycle (Ward and Wainwright, 1972). To evaluate this character, we have looked for a continuous connective tissue sheath over the inner and outer surfaces of the mantle muscle in histological sections. However, this approach did not always provide unambiguous results. Connective tissue is present on the mantle of all cephalopods and the difference between a continuous, uniform "tunic" and an irregular layer was not always clear. Indeed, we were unable to clearly distinguish what could be intermediate states in *Sepia* and *Octopus*. Because *Nautilus* lacks a mantle-propulsion system, a necessary precursor to the development of a collagenous tunic, it has no relevant character state.

Character No. 39: Spermatophores with ejaculatory apparatus. Character states: 0 - present; 1 - sperm packets; 2 - encapsulated coil.
Comments. All coleoid cephalopods except the finned octopods have characteristic spermatophores that contain a complex ejaculatory apparatus (Figs. 13A, B, D). The finned octopods produce peculiar sperm packets (Fig. 13E). This one character probably represents a suite of modifications to the spermatophore and the glands that form them, setting the cirrates apart from other coleoids. *Nautilus* has a spermatophore that lacks an ejaculatory apparatus (Mikami and Okutani, 1981), is very different from that of cirrate octopods (Fig. 13C), and has been given a separate character state (state 2).

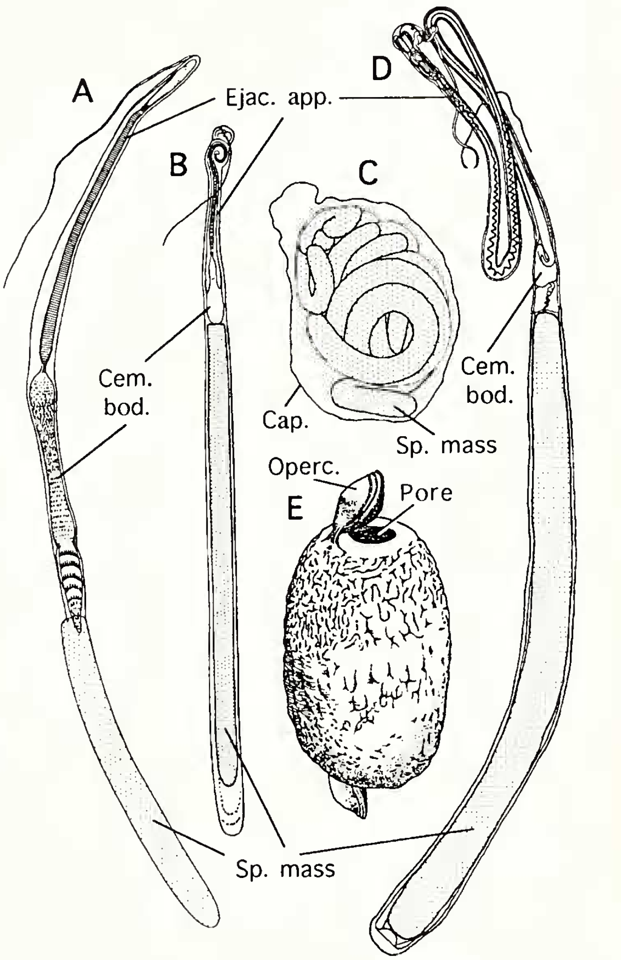

Fig. 13. Spermatophores. A. *Eledone* (modified after Marchand, 1912). B. *Loligo* (modified after Marchand, 1912). C. *Nautilus* (modified after Mikami and Okutani, 1981). D. *Vampyroteuthis* (modified after Hess, 1987). E. *Opisthoteuthis* (after Villanueva, 1992). (Cap., capsule; Cem. bod., cement body; Ejac. app., ejaculatory apparatus; Operc., operculum; Sp. mass, sperm mass).

Character No. 40: Superior buccal lobe. Character states: 0 - widely separated from brain; 1 - adjacent to brain; 2 - fused to brain.
Comments. The position of the superior buccal lobe relative to the supraesophageal mass of the brain varies greatly among different cephalopods depending largely on the distance between the buccal mass and the brain (Fig. 5). There are, however, three distinct states as defined above. State 0 is found in decapods and *Nautilus* (Figs. 5A, B), state 1 in *Vampyroteuthis* (Fig. 5C), and state 2 in octopods (Fig. 5D). J. Z. Young (1988: 255) misstated the condition in *Vampyroteuthis* as "the superior buccal lobes are joined

with the rest of the brain as in octopods" due to his examination of a distorted specimen (note the 90° turn in the esophagus in his fig. 5) that artificially compressed the superior buccal mass against the brain. In normal specimens the lobes are clearly separated medially. As a result we have given *Vampyroteuthis* a separate state which is intermediate between the decapod and octopod states and consider this character to have an "ordered" transformation series. A similar situation, with the exception of *Nautilus*, occurs with respect to the brachial lobe, but as this character is probably not independent from Character 40 in the coleoids, it was not used.

Character No. 41: Horizontal arm septa. Character states: 0 - absent; 1 - present.
Comments. Cirrate octopods have a horizontal septum that inserts on the circular muscle layer that forms the outer and thinner portion of the cyclindrical muscular wall of the arm. It is orally concave in cross-section and divides the muscular tube within each arm into oral and aboral regions. *Japetella* (Bolitaenidae) has a similar septum but its insertion on two membranes, extending in an oral-aboral plane well internal to the arm muscles, suggests that the cirrate and bolitaenid structures are derived independently.

Character No. 42: Paired digestive gland duct appendages. Character states: 0 - single; 1 - paired.
Comments. The digestive gland duct appendages (DGDA) are glands that attach to the ducts of the digestive glands. In decapods they are spread along the long ducts to form paired, multilobed structures (Figs. 8E, F) while in *Vampyroteuthis* and the octopods they are compacted next to the digestive gland in a single (unpaired) structure (Figs. 8B, D, 9). Although there is some variation in the Oegopsida, the organs always remain paired even where occasionally compacted against the digestive gland. Because *Nautilus* lacks DGDA, it has no relevant character state.

Character No. 43: Relative positions of the DGDA and the nephridial coelom. Character states: 0 - DGDA lies in the nephridial coelom; 1 - DGDA not in the nephridial coelom.
Comments. The DGDA can be suspended within a branch of the nephridial coelom and intimately covered by the coelomic lining (Figs. 8E, F) or lie outside the coelom and separated by, at least, several tissue layers from the coelom (Figs. 8B, D, 9). *Nautilus* lacks a relevant character state.

Character No. 44: Head width index. Character states: 0 - 0.49; 1 - 0.5-0.99; 2 - 1.0-1.49; 3 - 1.5-1.99; 4 - 2.0-2.49; 5 - 2.5-2.99; 6 - 3.0-3.49; 7 - 3.5-3.99; 8 - 4.0-4.49; 9 - 4.5-4.99.
Comments. This character relates head width to eye size by measuring the number of eye radii that separate the eyes. States were assessed by measuring the head width and the lens diameter. The eye radius was then calculated and doubled for subtraction from the head width. This is a continuous character that has been converted to a discrete character by dividing the range of the character into equal segments (Fig. 14). The definitions were compromised in groups (some sepioids and cirrate octopods) with a dorsal tilt to the eyes, and therefore, this character was excluded from the analysis.

Character No. 45: Gill filament attachment. Character states: 0 - inner and outer filaments free; 1 - outer filaments attached; 2 - inner and outer filaments attached.
Comments. In coleoids the gill filaments often are attached to the gill base surrounding the branchial gland by triangular membranes that are supported by slender cartilaginous rods (Figs. 11A, C, D). The length of the rod determines the distance of the filament from the branchial gland. The length of the rod varies with the position along the gill, the side of the gill, and the taxon. When the rod is absent in coleoids, the filament is defined as "attached" (Fig. 11E) and, in some cases, the difference between attached and free is slight. The gills of *Nautilus* are comparable to those of coleoids but lack a branchial gland and supporting rods to the filaments (Fig. 11B). The muscular triangular membranes broadly separate the tips of the filaments from the muscular base that occupies the position of the branchial

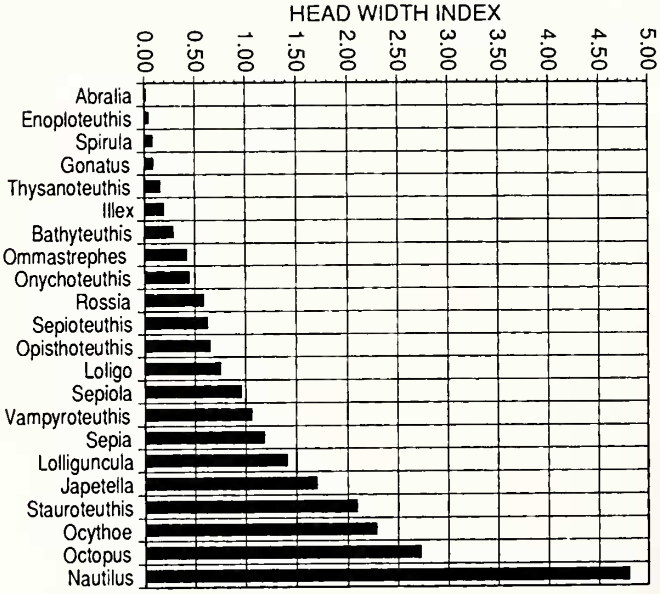

Fig 14. Histogram showing head-width index values for 22 taxa (Character 44).

gland in coleoids. As a result, we coded *Nautilus* as state 0. We had difficulty evaluating the character states in preserved animals and have concerns whether the states are adequately defined. While our attempt to determine and survey states is presented in the data matrix, we excluded this character from the analysis.

Character No. 46: Digestive gland. Character states: 0 - multiple digestive glands; 1 - two separate digestive glands (unipaired); 2 - digestive glands fused (single gland).
Comments. In coleoids the digestive gland consists of either two separate lobes or a single lobe. Separate but adjacent digestive glands can appear to be a single organ but are separated by a membrane and, in fresh specimens, can be pulled apart without damage to either organ. The definition of "separate" requires the lobes to be separate over their entire length. Within the coleoids, the appearance of two anlagen of the digestive gland in the embryos of *Loligo* and the presence of two digestive gland ducts in all coleoids indicate that unipaired glands (state 2) is the plesiomorphic state.

Character No. 47: Longitudinal muscle on mantle. Character states: 0 - present; 1 - absent.
Comments. We systematically sectioned the mantle in the region of the mantle-locking apparatus for the presence of a layer of longitudinal muscles. Generally a thin layer of longitudinal muscles was present external to the circular muscles on the outer surface. The longitudinal layer, however, is often discontinuous at least in the region surveyed and in a few families was absent.

Character No. 48: Position of vena cava relative to intestine. Character states: 0 - intestine passes ventral to vena cava; 1 - intestine passes dorsal or anterior to vena cava.
Comments. The cephalic vein extends posteriorly from the head along or near the ventral surface of the visceral mass until it splits to form the two branches of the vena cava. The intestine, arising from the visceral nucleus passes dorsal or anterior to this bifurcation (Figs. 8E, F) or, in some cases, passes posterior then ventral to the bifurcation and, as a result, traps the vena cava within the U-shape of the digestive tract (Figs. 8A, B, 9). In preserved specimens the cephalic vein and vena cavae often have collapsed and cannot be followed. As a result, we generally used the position of the intestine relative to the position of the renal appendages as an indicator of the character. In *Nautilus* the terminal portion of the intestine lies on the ventral mantle wall rather than on the visceral mass and is thereby separated from the vena cava (Griffin, 1900). As a result, this character is not applicable to *Nautilus*.

Character No. 49: Posterior salivary gland. Character states: 0 - absent; 1 - posterior to brain; 2 - on or in buccal mass.
Comments. The posterior salivary glands generally lie posterior to the cephalic cartilage. However, Aldred *et al.* (1983) found that in *Cirrothauma* a single gland is present and it lies within the buccal mass. Ebersbach (1915) reported a similar situation for *Grimpoteuthis umbellata* (Fischer, 1883) (his *Cirroteuthis umbellata*, see systematic comments in Voss, 1988). This character was surveyed as a possible synapomorphy for the cirrates. *Nautilus* lacks posterior salivary glands.

Character No. 50: Position of gonad relative to the VP coelom. Character states: 0 - gonad mostly within the coelom; 1 - less than 50% within.
Comments. In most cephalopods, the gonad, except for its attachment sites, lies mostly within the VP coelom, that is, it is covered by the coelomic lining (Figs. 1A, D). In octopods, however, the gonad lies mostly outside the coelom in a gelatinous milieu (Figs. 1B, C, E). Unfortunately, we had difficulty in incirrate octopods in determining how much of the gonad was covered by coelomic lining although it appeared to be greater than 50%.

In animals as complex as cephalopods numerous additional characters that have potential phylogenetic value at this level remain to be identified and surveyed. We mention four that we were unable to survey.

(1) Funnel-locking apparatus (Fig. 10A). In many cephalopods a specialized locking apparatus locks the funnel to the inner surface of the mantle. The locking apparatus occurs in decapods and some octopods and is probably convergent in these two groups. We suspect that in decapods the funnel component has a cartilaginous base that is lacking in octopods. However, even if this proves to be a valid distinction, it cannot be polarized by the condition in *Nautilus*. We originally attempted to apply this definition to the mantle component of the locking apparatus but found a large variety of structures with cartilage only rarely being present.

(2) Suprabrachial commissure (Fig. 5D). Most octopods have a strong commissure that loops dorsal to the esophagus and connects the lateral regions of the left and right brachial lobes of the subesophageal region of the brain (Aldred *et al.*, 1983). In cirrate octopods this commissure lies beneath the posterior buccal lobe but is separated from it by connective tissue. A corresponding commissure exists in *Vampyroteuthis* but is small and lies just beneath the posterior buccal lobe (pers. obs.). A counterpart is unknown in the decapods. Surprisingly this commissure appears to be lacking in *Japetella* (J. Z. Young, 1977). Unfortunately this is another character that cannot be polar-

Table 2. Data matrix for 50 characters and 17 taxa. Asterisk indicates character used in this study; slash indicates two character states present.

	1-5					6-10					11-15					16-20					21-25				
				*		*	*	*	*	*							*	*		*	*				*
Bathyteuthidae	0	0	1	0	2	0	1	2	0	1	2	1	1	1	1	0	0	0	1	0	0	1	1	1	1
Enoploteuthidae	0	0	1	0	2	0	1	2	0	1	1	1	0	1	0	0	0	0	1	0	0	0	1	1	1
Gonatidae	0	0	1	0	2	0	1	2	0	1	2	2	0	1	0	0	0	0	1	0	0	1	1	1	1
Loliginidae	0	0	1	0	2	0	1	2	0	1	1	1	0	1	0	0	0	0	1	0	0	1	1	1	1
Ommastrephidae	0	0	1	0	2	0	1	2	0	1	1	1	0	1	0	0	0	0	1	0	0	1	1	1	1
Onychoteuthidae	0	0	1	0	2	0	1	2	0	1	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1
Sepiidae	1	0	0	0	2	0	1	2	0	1	2	2	0	1	1	0	0	0	1	0	0	1	1	0	1
Sepiolidae	0	0/1	1/3	0/4	2	0	1	2	0	1	1/2	1/2	1	0	0/1	0	0	0	1	0	0	1	1	0	1
Spirulidae	1	1	0	2	2	0	1	2	0	1	2	2	1	1	1	0	0	0	1	0	0	1	1	0	3
Thysanoteuthidae	0	0	1	0	2	0	1	2	0	1	1	1	0	1	0	0	0	0	1	0	0	1	1	1	1
Bolitaenidae	0	1	3	4	0	2	0	0	2	0	0	0	1	0	1	1	2	1	0	1	1	0	0	1	2
Octopodidae	0	1	2	3	0	2	0	0	2	0	0/1	0/1	1	0	1	1	2	1	0/1	1	1	0	0	1	2
Ocythoidae	0	1	3	4	0	2	0	0	2	0	1	1	1	0	0	0	2	1	0	1	1	0	0	1	2
Stauroteuthidae	0	1	2	1	0	2	0	0	2	0	0	0	0	0	1	1	1	1	0	1	1	0	0/1	2	2
Opisthoteuthidae	0	1	2	1	0	2	0	0	2	0	0	0	0	0	1	1	1	1	0	1	1	0	0	2	1/2
Vampyroteuthidae	1	0	1	0	0	1	0	1	1	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0
Nautilidae/Ancestor	1	?	0	?	1	0	0	?	?	?	?	?	?	?	?	?	?	0	0	0	0	1	0	0	?

	26-30					31-35					36-40					41-45					46-50				
	*		*	*		*	*	*	*	*	*			*	*	*		*					*		
Bathyteuthidae	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0	1	0	0	0	2	0	1	1	0
Enoploteuthidae	0	0	0	0	1	1	0	0	0	1	0	1	1	0	0	0	1	0	0	0	2	0	1	1	0
Gonatidae	0	0	0	0	1	1	0	0	0	1	0	1	1	?	0	0	?	0	0	0	2	1	1	1	0
Loliginidae	0	0	0	1	0	1	0	0	0	1	0	1	1	0	0	0	1	0	1/2	0	2	0	0	1	0
Ommastrephidae	0	0	0	0	1	1	0	0	0	1	0	1	1	0	0	0	1	0	0	0/1	2	1	1	1	0
Onychoteuthidae	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	2	0	1	1	0
Sepiidae	0	0	0	1	0	1	0	0	0	1	0	1	?	0	0	0	1	0	2	0	1	0	0	1	0
Sepiolidae	1	0	0/1	1	0	1	0	0	0	1	0	0	1	0	0	0	1	0	1	0	2	0	0	1	0
Spirulidae	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	1	0
Thysanoteuthidae	0	0	0	0	1	1	0	?	?	1	0	1	1	0	?	0	1	0	0	0	2	1	1	1	0
Bolitaenidae	1	1	1	2	1	0	1	2	2	0	1	0	0	?	2	0	0	1	3	2	2	0	1	1	0
Octopodidae	1	1	1	2	1	0	1	2	2	0	1	0	?	0	2	0	0	1	5	2	2	0	1	1	0
Ocythoidae	1	1	1	2	1	0	1	2	2	0	1	0	0	0	2	0	0	1	4	1	2	0	1	1	0
Stauroteuthidae	1	1	1	0	0	0	1	2	2	0	0	0	0	1	2	1	0	1	4	0	2	0	1	2	1
Opisthoteuthidae	1	1	1	0	0	0	1	?	2	0	0	0	0	1	2	1	0	1	?	2	2	?	1	0	1
Vampyroteuthidae	2	0	0	0	1	0	0	1	1	1	0	0	0	0	1	0	0	1	2	0	2	0	0	1	0
Nautilidae/Ancestor	?	0	?	?	1	2	0	?	?	1	?	0	?	2	0	0	?	?	9	0	0	0	?	0	0

ized by *Nautilus*.

(3) Genital pocket. The genital pocket is an invagination of the integument lining the mantle cavity that surrounds the accessory spermatophore organs. Absence of a genital pocket in male cirrates could be a synapomorphy for this group. This is one of a probable suite of characters associated with the degeneration of spermatophore structure.

(4) Dorsal lobe of the nephridial sacs (Figs. 8A-D). These lobes (see Character 19) could prove to be a synapomorphy of the Vampyromorpha and Octopoda but are difficult to survey in preserved material.

ANALYSIS

We surveyed 50 characters in 17 families and these data are presented in Table 2. We eliminated four of these characters (Nos. 13, 38, 44, 45) from the analysis because of potential errors related to questionable definition of character states or accuracy of surveying the states. We also eliminated seven characters (Nos. 1, 5, 22, 23, 27, 30, 47) after determining that the plesiomorphic state was "present" and the apomorphic state was "absent." For these characters we could not determine if losses represented homology or involved homoplasy. Polarity was determined for these by outgroup comparison on MacClade. Some other characters fell so obviously into this pattern (*e. g.* presence/absence of fins) that they were not surveyed. Characters with "fused" as the apomorphic state also presented a problem in distinguishing between homology and homoplasy. Three characters (Nos. 19, 42, 46) were eliminated on this basis as their plesiomorphic condition was the unfused state (polarity for Character 19 based on outgroup condition and for 46 on ontogeny). We further eliminated

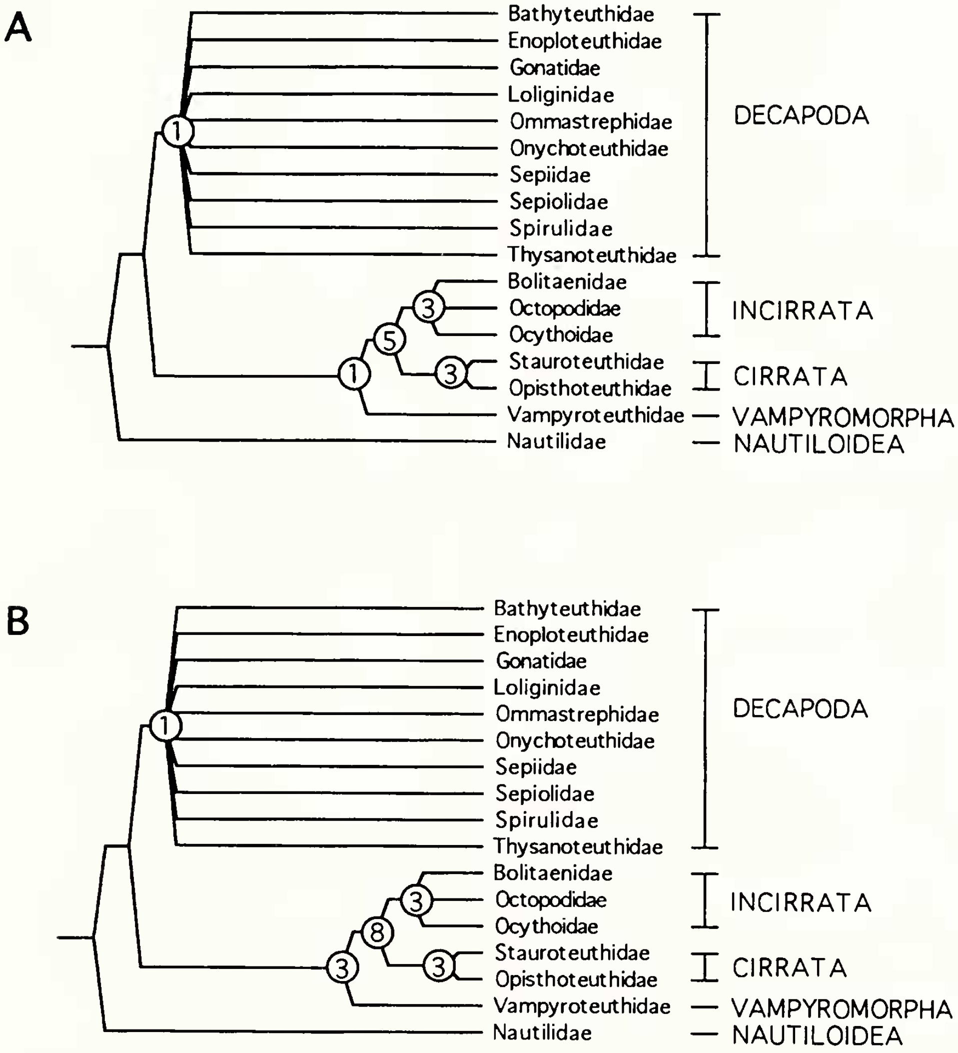

Fig. 15. Strict consensus of shortest trees from PAUP search of data set with 25 characters (14 trees; tree length 46). Numbers at internal nodes represent Support Indices. Indices of shortest trees: consistency index 0.98; homoplasy index 0.09; retention index 0.99; rescaled consistency index 0.97. Mickevich's consensus information from the consensus tree = 0.312. A. All character states unordered (Analysis I). B. Three characters with states ordered, others unordered (Analysis IIA). Bootstrap values (1,000 replicates) for nodes are: decapod node 70, octopod/vampire node 98, octopod node 100, incirrate node 97, cirrate node 97.

three characters (Nos. 2, 3, 50) because they might not be completely independent from other characters (*i. e.* Nos. 4, 4, 20, respectively) due to some overlap in definitions. One character (No. 37) was eliminated as it varied only within a major group (Decapoda) and was, therefore, uninformative at the level of interest in this study. Seven characters (Nos. 11, 12, 14, 15, 16, 24, 48) exhibited homoplasy under all plausible phylogenetic rearrangement of the groups. The worst of these was Character 24 (branchial canal), a presence/absence character with "absence" in *Nautilus* presumably defining the plesiomorphic state. All rearrangements resulted in multiple homoplasy, varying from three independent derivations to three independent losses of branchial canals with the minimum homoplasy involving two convergences. Until these seven characters can be redefined to eliminate homoplasy, we eliminate them from analyses. This left 25 characters.

We first analyzed the data (Analysis I, PAUP, Fig. 15A) with all characters entered as "unordered." To determine the strength of the nodes we determined the support index (SI) for all internal nodes (Eernisse and Kluge, 1993). Decapod monophyly (SI = 1) was supported unambiguously by only a single character (No. 7, Arms IV). However, eight other characters that we were not able to polarize (Nos. 8, Sucker rings; 9, Sucker stalks; 10, Sucker symmetry; 17, Fin cartilage; 31, Oviducal gland symmetry;

33, Photosensitive vesicles; 34, Subfrontal lobes; 43, DGDA/nephridial coeloms) have states that are, presently, found exclusively in the decapods and in all the decapods. In this first analysis only a single unambiguous character (No. 18, Statocyst outer capsule) change supported the vampyromorph/octopod node (SI = 1). Four additional characters (Nos. 10, Sucker symmetry; 17, Fin cartilage; 31, Oviducal gland symmetry; 43, DGDA/nephridial coeloms) could support this clade depending on which states prove to be plesiomorphic within coleoids. Monophyly of the Octopoda (SI = 5) was supported by five characters (Nos. 20, Visceropericardial coelom; 21, Dorsal mantle cavity; 28, Nuchal cartilage; 32, Oviducal gland position; 35, Arm-mantle muscle) and, potentially seven more (Nos. 6, Arms II; 8, Sucker rings; 9, Sucker stalks; 25, Mantle septum; 33, Photosensitive vesicles; 34, Subfrontal lobe; 40, Superior buccal lobe) depending on how polarity is resolved. The Cirrata (SI = 3) were supported by unambiguous changes in three characters (Nos. 39, Spermatophores; 41, Horizontal arm septa; 49, Posterior salivary glands) and one potential unpolarized character (No. 4, Shell shape). The Incirrata (SI = 3) were supported by unambiguous changes in three characters (Nos. 17, Fin cartilage; 29, Cornea; 36, Arm III hectocotylus) although the first is a "non-applicable" state resulting from fin loss.

We next analyzed the data (Analysis IIA, PAUP, Fig. 15B) after ordering three characters (Nos. 6, Arms II; 34, Subfrontal lobe; 40, Superior buccal lobe) whose evidence warrants this restriction (see Comments under each character). We consider this to be our best estimate of the phylogeny at this time. Topology and tree length did not change from the previous analysis. However support for some clades improved. Support for the decapod clade was unchanged, while the SI for the vampyromorph/octopod node increased to 3 from the additional unambiguous changes in two characters (Nos. 6, 40). Character 34 did not contribute to this node due to its ambiguous polarization at the coleoid node. All three ordered characters supported additional unambiguous character changes for the Octopoda which increased the SI to 8. Support for the Cirrata and Incirrata were unchanged. In both analyses the low degree of homoplasy in the data set utilized apparently resulted in the SI being identical to the number of unambiguous character changes at each node. We ran this same data set in Hennig86 (Analysis IIB) which provided the same topology for the six internal nodes (14 trees, tree length = 46, consistency index = 0.97, retention index = 0.99).

DISCUSSION

Analysis II provided marginal support for monophyly of the decapod clade (one character). However, the large pool of characters with states diagnostic of decapods but unpolarized suggests that additional support is likely. The vampyromorph/octopod clade seems reasonably well supported by three characters although some of these carry assumptions. Four unpolarized characters offer the possibility of additional support. The monophyly of the Octopoda was very well supported by eight characters with possible additional support from another three unpolarized characters.

Although monophyly of decapods, cirrate and incirrate octopods (Vampyromorpha is monotypic) was supported, we emphasize that not all families were included in our examination of these higher taxa. While we expect these higher taxa were adequately representated, confirmation from all families is needed.

The tree resulting from Analysis II rests on only 16 characters involving 18 character state changes. Ten characters defined the decapod, octopod, and octopod + vampyromorph clades. An additional six characters defined the two octopod clades. The remaining nine characters were effectively neutral (*i. e.* they neither added to nor substracted from support for the internal nodes). One of our primary obstacles in this study has been our inability to polarize many of the characters at the basal coleoid node. Because of this problem, eight of the nine neutral characters were "neutralized" and six of the other characters were only partially effective. As expected, PAUP analysis of the 16 characters gave the identical tree with identical SI values to that of Analysis II (tree length, of course, was shorter: 24) while analysis of the nine neutral characters resulted in a completely unresolved consensus tree.

In future analyses of decapod families with more nodes and a more complex hierarchy of nodes, emphasis must be placed on thoroughly understanding the interrelationships of characters that will enable determination of the basal clades upon which much of the polarization at more resolved nodes must rest. Efforts should, therefore, be placed on locating characters that have counterparts in outgroups (or can be polarized by ontogeny/paleontology), and that do not involve loss as the synapomorphy. Multistate characters in which evolutionary pathways can be reconstructed would be especially valuable. Homoplasy in these "basal" characters is dangerous but elimination of homoplasic characters is not only wasteful of any useful information they can contain but could be impossible, in a more complex and poorly understood phylogeny, by the method used here (*i. e.* recognition of which characters are homoplastic on the basis of "implausible relationships"). Only a thorough understanding of the relationships among character states through detailed study can guard against this pitfall. We simply argue in favor of an approach to phylogenetic studies by the methodology referred to by Mickevich (1995) as "synapomorphic cladistics" and long-recognized by many others (*e. g.* Bryant, 1989).

ACKNOWLEDGMENTS

We thank Clyde Roper (USNM) for providing space, specimens, and facilities for undertaking much of this work, Michael Sweeney (USNM) for his help on various aspects of the work, and Mary Mickevich (National Systematics Laboratory, USNM) for her comments and suggestions. R. E. Y. is also indebted to Helen Martins (University of the Azores) for providing laboratory space and facilities during a stay in her laboratory; James Childress (University of California, Santa Barbara) for allowing participation in one of his cruises; officers and crews of the HOKUSEI MARU (University of Hokkaido) and Moana Wave (University of Hawaii) for material gathered during cruises.

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Date of manuscript acceptance: 15 February 1996